Chapter 16

Population Models for Atlantic Loggerheads:

Past, Present, and Future

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Population models can be useful tools for decision makers because they can quantify the relative effectiveness of different management options (Heppell et al. 2000b). This is particularly critical for long-lived species such as sea turtles, where a scientist's entire career may only span one or two turtle generations. Researchers have modeled the dynamics of a wide range of species and have addressed a variety of management applications, from simple biomass-based models in fisheries (Hilborn and Walters 1992) to population viability analysis (Beissinger and Westphal 1998; Boyce 1992) for endangered species. In all cases, the models serve as hypothesis-testing tools, where a series of potential outcomes is assessed based on a set of parameters and assumptions. While some models attempt quantitative predictions of population dynamics, such as the extinction probabilities in many population viability analyses, these models also serve as heuristic tools to compare the relative magnitude of population changes, even when quantitative predictions are not possible (Groom and Pascual 1998).

Quantitative demographic models require large amounts of data on life-stage–specific survival, growth and fertility, migration, and effects of environmental variability on these parameters (Groom and Pascual 1998). Long-term mark-recapture studies, such as those conducted in Australia (Chaloupka, Chapter 17 this volume), have allowed the construction of statistically based models that can test quantitative hypotheses. But data sets of this quality and magnitude are relatively rare for sea turtles. Population demography for Atlantic loggerheads, which began in the 1970s, continues to suffer from a lack of long-term data on critical demographic rates. These limited data have required simpler models that generally produce qualitative, rather than quantitative, predictions. Although results from analyses of such models require qualitative interpretations due to uncertainty in parameter estimates and simplifying

assumptions, they have provided important insights into the relative effects of various management actions and have guided sea turtle management policies in the United States (Heppell et al. 2000b).

Models of the Past

Frazer's Life Tables

Frazer (1983a) constructed a life table for loggerheads for several reasons. First, the life history of loggerheads had never been fully described. He expected that management could be improved if scientists' understanding of the loggerhead's demographic characteristics were synthesized. Second, he believed that the effectiveness of conservation efforts could be evaluated only by comparing future changes with detailed information on the loggerhead's current status. Thus, it seemed prudent to describe their present life-history characteristics in conventional terms so that any subsequent changes might be easily recognized and assessed using standard models. Third, Frazer felt that estimates of age at maturity, survivorship, and fecundity were of intrinsic interest to students of life-history evolution, irrespective of their utility in management and conservation plans. As Wilbur (1975) pointed out, the analysis of long-lived, iteroparous species constituted one of the most serious deficiencies in the study of life-history tactics. Thus, Frazer's (1983a) goal was simply "to describe the loggerhead's life history as completely as possible" by compiling all data available at the time for the western Atlantic. Of necessity, Frazer's (1983a) analyses were fraught with assumptions, as we shall see below.

The most reliable inputs to Frazer's (1983a) analyses were the empirical estimates of adult female survival and fecundity, which were based on a 17-year project at Little Cumberland Island, Georgia, where the beach was patrolled at approximately hourly intervals from dusk until dawn each night of the nesting season. Frazer (1983a, 1983b) estimated adult female survival with and without adjustments for tag loss. The hourly patrols allowed researchers to identify and mark most individual females so clutch frequency could be accurately assessed. Because the researchers transferred eggs from natural nests into a fenced location in a natural sand

dune, they also counted eggs to determine clutch sizes (Frazer 1983a; Frazer and Richardson 1985). By eliminating the first five years of tagging data, Frazer (1983a) was able to estimate the reduced clutch size, reduced clutch frequency and smaller body size of "neophytes" (first-time nesters). After five years of saturation tagging on the beach, Frazer assumed that turtles arriving at the site without tags or tag scars were nesting for the first time. Tagging data also allowed Frazer to estimate return or remigration intervals, which were important for assessing age-specific survival and fecundity because not all females appear on the beach each year.

These estimates of adult female survival and fecundity also allowed Frazer to estimate the overall survival rate, from egg to maturity, necessary to maintain either a stable population or a population declining at the observed rate of approximately 3% per year at Little Cumberland Island (Frazer 1983a, 1986). Once this estimate was available, the remaining tasks were to estimate juvenile survival and, hence, determine the shape of the survivorship curve between hatching and adulthood.

At the time there were no reliable means available for aging loggerheads. Frazer (1983a; Frazer and Ehrhart 1985) used information on growth rates of juvenile and adult loggerheads in Florida waters to construct length-at-age growth curves for loggerheads. Unfortunately, no data were available for juveniles smaller than 50 cm in carapace length. Frazer (1983a) rejected the practice of using the size of the smallest known nesting female as indicative of typical size at maturity for the population. In the absence of other data, he had little recourse other than to assume that loggerheads matured at a size slightly smaller than the mean size of nesting females (i.e., the mean size of nesting females minus one standard deviation). This yielded an estimate of 22 years for age at maturity. Frazer (1983a, 1987) also used the growth curve to assign ages to two groups of juvenile loggerheads: 607 carcasses washed ashore on Georgia beaches and 196 juveniles caught in shrimp trawls in waters off the Atlantic coast of Florida. After assigning ages to the turtles with the growth curve, Frazer (1983a, 1987) conducted a catch-curve analysis to estimate survival of juvenile loggerheads from 8 to 16 years old.

Once estimates were available for loggerheads 8–16 years of age and for nesting females, all that remained was to connect up the survivorship curves by interpolation for those turtles for which no empirical information was available (i.e., from hatchling to age 8 and from age 16 to 22). Frazer (1983a) did this under two scenarios: (1) a stable population and (2) a population declining at a rate of 3% per year, which was the average rate of decline in nesting females appearing on Little Cumberland Island, Georgia, in 1963–1980.

Three major issues merit mention. The first two are vagaries introduced into the life table due to Frazer's simplifying assumption that all loggerheads reach maturity at the same age: (1) the estimate of average fecundity at age 22 is inflated because all females are assumed to nest in the year they attain maturity, and (2) few Little Cumberland loggerheads ever return to nest at an interval of only one year, so the per capita fecundity at age 23 seems unnaturally low (four female hatchlings per year). Lastly, most modern readers will question the wisdom of combining information from the Florida and Georgia loggerhead populations in the western Atlantic. While researchers now know that loggerheads in Florida and those in Georgia probably represent two distinct breeding aggregations (Bowen et al. 1993), the genetic data were not sufficient to discriminate between loggerheads nesting in the two areas when Frazer (1983a) constructed his life tables.

Matrix Models

While Frazer's life table provided the first model for loggerhead life history, it was not clear how it might be used to help managers reverse the declines in loggerhead populations. Various management actions were in place or had been proposed, including nest protection, hatcheries, and fishing gear modification to reduce large turtle mortality in shrimp trawls. Modifications of trawls to release sea turtles were highly controversial among conservationists, managers, and the shrimping industry because it was not clear if these modifications were truly necessary to promote population recovery.

To assess this, Crouse et al. (1987) collapsed Frazer's 54 age-class life table into a 7 × 7 stage-classified transition matrix. This modeling strategy recognized the uncertainty in ages associated with each stage class and the underlying size-based structure of Frazer's life table. In the stage-based model, each row and column of the matrix represented one of Frazer's seven life stages: eggs/hatchlings, small (oceanic) juveniles, large juveniles, subadults, novice breeders, first-year remigrants (the small proportion of females that return to nest in the year following their first nesting migration), and mature breeders. The matrix included three parameters for each stage: P_i, the annual probability of surviving and remaining in a stage; G_i, the annual probability of surviving and growing into the next stage; and F_i, the per capita annual production of daughters (Equation 1). To read the transition probabilities of the matrix, think of individuals growing from a column (j) to a row (i). Reproduction, the production of eggs and hatchlings by females in each stage, occurs in the top row of the matrix. For example, column 3 of the Crouse et al. matrix indicates that, in a given year, 1.5% of large juvenile female turtles grow to become subadults while 66% of them survive but remain in the large juvenile stage (Equation 2). Turtles that die (100 − 66 − 1.5 = 32.5%) "disappear" from the model. Large juveniles do not reproduce, so a zero appears in the top row of the large juvenile column.

$$\begin{bmatrix} P_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6 & P_7 \end{bmatrix} \quad (1)$$

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 127 & 4 & 80 \\ 0.675 & 0.737 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.049 & 0.661 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.015 & 0.691 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.052 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.809 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.809 & 0.809 \end{bmatrix} \quad (2)$$

Caswell (Caswell 2000; Caswell and Werner 1978) has illustrated many advantages to presenting life table information in matrix form. The eigenvalues and eigenvectors of a transition

matrix reveal the asymptotic population growth rate (λ, where $\ln[\lambda]$ = r, the population's intrinsic rate of increase), stable age distribution (w) (the constant proportion of individuals in each stage once the model has reached the equilibrium growth rate, λ, and stage-specific reproductive values (v) (the relative value of current and future reproduction by females in each stage).

Because the model did not incorporate annual variability in vital rates and included a number of uncertainties, using it to predict population size was inappropriate. Instead, Crouse et al. (1987) ran a series of "what if" scenarios to examine the relative impacts of increasing or decreasing the survival rate of each life stage. They found that increasing the annual survival rate of eggs and hatchlings to 100% had virtually no effect on population growth; in spite of an increase in the number of survivors in each annual cohort, the population continued to decline. Increasing the survival rate of small juveniles, large juveniles, subadults, and mature breeders did result in positive population growth. Relative to changes in other model parameters, population growth rate was increased most from a proportional increase in large juvenile annual survival. Thus, through simulation, Crouse et al. (1987) determined the sensitivity of population growth to changes in stage-specific annual survival.

Analytical methods for obtaining similar results were developed by Caswell et al. (1984) and further explored by de Kroon et al. (1986). A proportional sensitivity analysis, called elasticity analysis, is used to calculate the proportional changes in λ expected from proportional changes in each model parameter of a matrix (A). Elasticities ($E_{i,j}$) are easily calculated using the stable age distribution and reproductive value vectors of A:

$$E_{i,j} = \frac{\partial \lambda}{\partial A_{i,j}} \frac{\lambda}{A_{i,j}} = \frac{v_i w_j}{\langle v, w \rangle} \qquad (3)$$

where $\langle v, w \rangle$ is the scalar product of the two eigenvectors, or $\Sigma v_i w_i$ (Caswell 2000). This analysis was applied to the Crouse et al. (1987) model and has been used in subsequent loggerhead models (Crowder et al. 1994; Heppell et al. 1996a). It is one of the most useful results

obtained from a deterministic (i.e., non–time varying) matrix model without density dependence (de Kroon et al. 2000). For management applications, λ is treated as an index, and it is assumed that perturbations that cause large changes in λ are more effective than perturbations that cause small changes in λ.

Stage-classified models are very useful when life stages are based on size or shifts in diet or habitat over the developmental period, but they do not capture population responses to time lags. Late age at maturity in sea turtles makes it particularly important to use an age-classified matrix for population projections, as perturbations that affect one life stage may take years to manifest themselves as population changes in subsequent life stages. An age-based model presented in Crowder et al. (1994) showed that nesting female abundance would not increase exponentially with an increase in survival due to small cohorts that experienced years of heavy shrimping. Transient "waves" in abundance can be expected as cohorts of different sizes reach maturity, even without the added variance expected from environmental stochasticity. Thus, sea turtle population growth rates are notoriously difficult to measure, particularly when censuses are limited to nests and nesting females, and results of conservation actions may not be readily apparent for many years.

Misinterpretations of Matrix Model Results

Unfortunately, model results can be misinterpreted in spite of careful notation of assumptions and caveats. The low elasticities calculated for hatchling loggerheads give the wrong impression that egg and hatchling survival has no impact on population growth. Elasticities are relative measures; what the results actually say is that a proportional increase in egg survival, say 5%, will have a much smaller impact than a 5% increase in large juvenile annual survival (Caswell 2000). These results do not say that eggs are unimportant; obviously, egg survival must be maintained at a high enough level to assure that there will be recruitment to the adult population (Heppell 1997). It may well be that management efforts can increase egg

survival and large juvenile survival by different percentages, but the results of Crouse et al. (1987) also show that an increase in egg survival, no matter how large, will fail to prevent population decline in the model. However, an increase in cohort size will increase the population size, at least over the short term. Once the primary anthropogenic mortality sources that are the causes of population decline have been eliminated, boosting the population through larger cohort sizes can be highly beneficial. For example, the current rapid rate of increase observed in Kemp's ridley nests is likely due to a combination of reduced mortality through turtle excluder devices and a much higher egg survival rate than would be expected in an unmanaged population (TEWG 1998).

The life history of loggerheads and other sea turtles gives rise to a common pattern of low hatchling elasticity, high juvenile or subadult elasticity, and somewhat lower adult elasticity (Heppell 1998). In the loggerhead model, the large juvenile stage is eight years in length, whereas the egg/hatchling stage is only one year in length. Thus, an increase in large juvenile survival affects several age classes. In a long-lived, late-maturing species, adults make up a small proportion of the population; thus, a proportional change in the survival rate of adults will have a smaller effect on population growth. This says nothing about the relative value of individual adults versus juveniles. Adult longevity is of critical importance in loggerheads because females must, on average, survive to reproduce several times in order to replace themselves. The "value" of adults is about 600 times that of hatchlings according to the reproductive values calculated by Crouse et al. (1987) and Crowder et al. (1994). The adult reproductive value is also about 100 times that of large juveniles, so the loss of a single adult has a much greater overall effect than the loss of a single juvenile. However, because elasticities measure the proportional effect of a change in the survival rate, which affects all individuals in a stage on a proportional basis, the elasticity of population growth to a change in large juvenile survival is much greater than that expected for the same change in adult survival.

Effects of Model Results on Policy

The loggerhead models provided managers with new insights with which to prioritize management and research activities. Prior to development of the 1987 loggerhead model, management and research tended to focus on the most obvious problems (losses of nests and hatchlings to predators and erosion) or the most accessible life stages (nesting behavior, fecundity, and hatch success). Researchers knew that turtles were caught and drowned incidentally to various fisheries, including shrimp trawl fisheries, but measures to reduce turtle mortality had been unpopular with the industry. Because researchers lacked information on the relative importance to population growth of mortality at different stages, most management efforts focused on the mitigation measures that were easiest to implement: protection of nests and eggs. But this focus relied on the tacit assumption that protecting nests would be adequate to mitigate for incidental losses to fisheries as well as for erosion and nest predation.

The results of Crouse et al. (1987) suggested that this assumption was invalid and provided key information contributing to the National Marine Fisheries Service (NMFS) decision to require turtle excluder devices (TEDs) in certain shrimp trawls at certain times of the year. This decision was tested, first in the courts (Louisiana vs. Verity 681 F. Supplement 1178 and 853 F, 5th Circuit Court 1988) and then in Congress (Public Law 100-478-October 7, 1988; Weber et al. 1995). In each case the science, including the findings of Crouse et al. (1987), was affirmed. A National Research Council panel, mandated by Congress specifically to reevaluate the decision to require turtle excluder devices, noted that ". . . analyses of populations and reproduction (Crouse et al. 1987) are especially useful for making decisions about conservation of sea turtles, because they help to identify life stages in which reduced mortality can have the greatest influence on the maintenance or recovery of endangered or threatened sea turtle populations" (National Research Council 1990:61).

In addition to a new emphasis on reduction of mortality in the older life stages, the models

suggested that increasing the survival of the earliest stages (eggs and hatchlings) may be a less effective conservation technique than was previously assumed (Crouse et al. 1987; Crowder et al. 1994; Heppell et al. 1996b). In 1994, the U.S. Fish and Wildlife Service (USFWS) and NMFS reoriented a long-term Kemp's ridley head-start program from rearing hatchlings for release to determining the relative survival of head-started to wild juveniles as a measure of the true effectiveness of head-starting (Eckert et al. 1994).

Finally, while still in the early stages, researchers and agencies have begun documenting and, to some extent, addressing mortality in other life stages. For example, longline fisheries are known to incidentally catch oceanic juvenile loggerheads, which have the second highest elasticity in the original loggerhead models. Pelagic longline takes of loggerheads and other sea turtles occur globally (Aguilar et al. 1995; Johnson et al. 1999; Nishimura and Nakahigashi 1990; National Marine Fisheries Service 2001; Witzell 1999), and the cumulative take of multiple longline fisheries that capture turtles from several life stages may be very high (Crouse 1999; NMFS 2001). Preliminary research has begun to investigate gear modifications that may reduce longline capture rates (Bolten et al. 1994; Ito and Machado 1999), but few changes have been required in the fisheries as yet. Recent court decisions have led to large spatial and temporal closures in the North Pacific to protect sea turtles from bycatch in Hawaii-based longline fisheries (Center for Marine Conservation et al. vs. National Marine Fisheries Service et al. Civil No. 99-00152). Although this case was driven primarily by concerns for the status of Pacific leatherbacks (Crowder 2000; Spotila et al. 2000), the closure will protect loggerheads and three other species of sea turtles as well.

New Information on U.S. Loggerheads

Research over the past 20 years has revealed new information on genetics, growth, the effects of turtle excluder devices, and other aspects of U.S. loggerhead biology. This information has important implications for existing and future population models.

Genetics

Based on mitochondrial DNA, there are at least four genetically distinct loggerhead nesting subpopulations in the western North Atlantic (Bowen 1995; Bowen et al. 1993; Encalada et al. 1998), and possibly there are more (Francisco et al. 1999; TEWG 2000):

1. The northern nesting subpopulation, occurring from North Carolina to northeastern Florida, above 29° N (with approximately 7,500 nests in 1998).
2. The southern Florida nesting subpopulation, occurring from 29° N on the eastern coast to Sarasota on the Gulf coast (with approximately 83,400 nests in 1998).
3. The Florida panhandle nesting subpopulation, occurring at Eglin Air Force Base and the beaches near Panama City, Florida (with approximately 1,200 nests in 1998).
4. The Yucatán nesting subpopulation (Márquez-M. 1990), occurring in Quintana Roo on the eastern Yucatán Peninsula, Mexico (with approximately 1,000 nests in 1998).

Genetic analyses indicate that turtles from several subpopulations mix on foraging grounds. Table 16.1 summarizes the estimated proportional contributions of the four identified subpopulations to foraging-ground assemblages as well as the proportional contributions of Mediterranean haplotypes.

Oceanic Stage Turtles

Loggerhead hatchlings originating from western Atlantic nesting beaches swim offshore into the currents and eddies of the North Atlantic gyre (reviewed by Bolten, Chapter 4 this volume). Small loggerheads have been found in the eastern Atlantic (Bjorndal et al. 1994; Bolten et al. 1994; Carr 1986, 1987; Maigret 1983) and in the Mediterranean Sea (Laurent et al. 1998). After 7–12 years in the oceanic immature life stage (Bjorndal et al. 2000), western Atlantic loggerheads return to nearshore waters and eventually settle into coastal habitats as neritic immatures. This ontogenetic shift is recorded in the growth layers of the humerus bone (Snover et al. 2000).

Growth

Growth rates may be specific to subpopulations (i.e., genetically different groups) and undoubtedly vary by foraging ground. Growth rates of loggerheads in the Bahamas and Florida are reported to be greater than growth rates of loggerheads to the north, where the northern subpopulation is disproportionately represented (Bjorndal and Bolten 1988; Braun-McNeill et al., in review; Klinger and Musick 1995; Mendonca 1981). In the seasonally temperate waters, these animals must migrate, but individual animals repeatedly return to the same developmental habitats in subsequent years. The slower growth rate of northern loggerheads may mean that they mature at a later age than their southern counterparts, and thus the northern subpopulation may be slower to recover than subpopulations with faster individual growth rates (Braun-McNeill et al., in review). Based on growth rates observed in North Carolina (Braun-McNeill et al., in review) and Virginia (Klinger and Musick 1995), the duration of the neritic stage (45–92 cm) would be nearly 25 years, which is much longer than would be estimated based on growth rates observed to the south.

Turtle Excluder Device Effects

The authors have generally assumed that mortality factors affect both juveniles and reproductive adults in proportion to their occurrence in near-shore and inshore neritic habitats; much less is known about the movements and habitats of nonreproductive adults. While turtle excluder devices have likely reduced near-shore mortality in shrimp trawl fisheries in the southeastern United States (Crowder et al. 1995), signs of recovery in the population remain mixed (TEWG 2000). New analyses indicate that current turtle excluder device openings in the southeastern United States are not adequate to release large loggerheads, including all reproductive animals (Epperly and Teas 1999). Turtle excluder devices are now required seasonally in the summer flounder trawl fishery south of Cape Charles, Virginia (61 FR 1846, January 24, 1996), but trawls are also used to fish for other species in waters where logger-

heads occur (flynet trawls, trawls north of Cape Charles, crab trawls, scallop trawls, etc.), and there is no reason to assume they are not taking turtles; limited data suggest some are (S. Epperly, pers. comm.). Likewise, bottom trawl fisheries for shrimp and other target species in other parts of the world are likely to incidentally capture and drown loggerheads and other sea turtle species wherever they coincide.

Updating the Models

Clearly, the "old" models of Frazer, Crouse, Crowder, and Heppell are lacking this new information. There are two alternatives to improving population models for Atlantic loggerheads: (1) use the same basic construct promoted by the earlier matrix models, but update the matrices with new information, or (2) start from scratch, building completely different models that incorporate information that cannot simply be added to the existing models. For this review chapter, the authors decided to examine the effects of increased stage length and potential "turtle excluder device effects" on modified matrix models. The updated models are still largely based on information gathered by Frazer (1983a, 1983b) and therefore best represent the northern nesting subpopulation.

The authors looked at two models with different stage lengths based on new growth rate information (Table 16.2). Model 1 includes the neritic immature stage lengths used in previous loggerhead models but adds one year to the oceanic stage, as predicted by growth estimates from young animals tagged in the Azores (Bjorndal et al. 2000). The age at first nesting in Model 1 is 23 years. Model 2 in composed of longer stage lengths than Model 1. A 10-year oceanic stage is predicted by the outer tail of the growth rate distributions calculated by Bjorndal et al. (2000). The longer neritic immature stages are based on newly calculated growth curves from tagged turtles in North Carolina (Braun-McNeill et al., in review). The age at first nesting in Model 2 is 35 years. The authors feel that the likely range of ages at first nesting for northern loggerheads has been bracketed by these two models, although additional research is needed to improve stage-length estimates.

Table 16.1.

Natal Origin of Foraging-Ground Loggerhead Sea Turtles (Proportional Contribution)

Foraging Area	Refs.	Life Stage(s)	N	Western North Atlantic				South Atlantic	Mediterranean
				Northern	Southern Florida	Florida Panhandle	Quintana Roo, Mexico	Brazil	Greece
Northeastern USA	8	Primarily neritic immature	82	0.25	0.59	0.00	0.16	0.00	0.00
Chesapeake Bay[a]	7	Primarily neritic immature	63	0.54	0.46	—	—	—	—
Pamlico and Core Sounds, North Carolina	1	Neritic immature	7	0.32	0.64	< 0.01	0.03	0.01	0.00
South Carolina[a]	11	Neritic immature	33	0.50	0.50	—	—	—	—
Georgia[a]	10	Neritic immature	97	0.59	0.41	—	—	—	—
Georgia	2	Neritic immature	192	0.24	0.73	—	0.03	0.00	0.00
Hutchinson Island, Florida	12	Neritic immature	109	0.10	0.69	—	0.20	—	—
Florida Bay	9	Neritic immature and adult	51	0.08	0.84	—	0.08	—	—
Mediterranean Sea[a]	4, 5	Unknown	59	—	0.57	—	—	—	0.43
Azores and Madeira	3	Oceanic immature	183	0.19	0.71	0.00	0.11	0.00	0.00

Western Mediterranean	6	Oceanic immature	59	0.02	0.45	—	—	—	0.53
Eastern Mediterranean	6	Oceanic immature	52	0.02	0.47	—	—	—	0.51
Eastern Mediterranean	6	Neritic immature and adult	58	—	—	—	—	—	1.00[b]

Source: Turtle Expert Working Group 2000.

Reference Key: 1. Bass et al. 1998. 2. Bass et al. 1999. 3. Bolten et al. 1998. 4. Bowen 1995. 5. Laurent et al. 1993. 6. Laurent et al. 1998. 7. Norrgard 1995. 8. Rankin-Baransky 1997. 9. Schroeder, unpubl. data. 10. Sears 1994. 11. Sears et al. 1995. 12. Witzell et al., in prep.

Note: Table values are proportional contributions. N = number (in sample).

[a]Studies were conducted before a full complement of genetic analyses of Atlantic nesting beaches was available.

[b]Includes rookeries of Turkey and Cyprus, in addition to Greece.

Western Mediterranean	6	Oceanic immature	59	0.02	0.45	—	—	—	0.53
Eastern Mediterranean	6	Oceanic immature	52	0.02	0.47	—	—	—	0.51
Eastern Mediterranean	6	Neritic immature and adult	58	—	—	—	—	—	1.00[b]

Source: Turtle Expert Working Group 2000.

Reference Key: 1. Bass et al. 1998. 2. Bass et al. 1999. 3. Bolten et al. 1998. 4. Bowen 1995. 5. Laurent et al. 1993. 6. Laurent et al. 1998. 7. Norrgard 1995. 8. Rankin-Baransky 1997. 9. Schroeder, unpubl. data. 10. Sears 1994. 11. Sears et al. 1995. 12. Witzell et al., in prep.

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[a]Studies were conducted before a full complement of genetic analyses of Atlantic nesting beaches was available.

[b]Includes rookeries of Turkey and Cyprus, in addition to Greece.

Table 16.2.
Stage Lengths Used in Updated Loggerhead Matrix Models

	Oceanic Immature 5–45 cm	Small Neritic Immature 45–72 cm	Large Neritic Immature 72–92 cm	Age at 92 cm
Model 1	8 years	6 years	8 years	23 years
Model 2	10 years	11 years	13 years	35 years

Methods

The model framework, as illustrated by the life cycle graph (Figure 16.1), is an adaptation of the five-stage model given by Crowder et al. (1994). Three major changes have been made. Eggs and hatchlings are no longer a separate stage—the survival rate from nest laying to entry into the ocean (0.6747 per year; Frazer 1986) is now included in the fertility term. The model has a prebreeding census, where turtles are "counted" just prior to nesting, requiring that fecundity be multiplied by survival at sea to age one to calculate the fertility term for the matrix (Caswell 2000):

$$F = \text{nests} \times \text{eggs} \times \text{sex ratio} \times \text{survival from egg to age one} \tag{4}$$

Reproduction parameters are the following: nests per female = 4.1; eggs per nest = 115 (TEWG 1998); and sex ratio = 0.5. Survival to age one is a fitted parameter, described below. The second major change in the model is incorporation of a variable remigration interval, based on tag returns at Little Cumberland Island (Richardson et al. 1978). The proportion of females returning to nest after one, two, three, four, or five years is 3%, 56%, 31%, 7%,

and 3%, respectively. Variable remigration intervals can have a major impact on nesting female abundance through time (M. Chaloupka, pers. comm.). All nesting females, regardless of remigration interval, produce the same number of one-year-old female offspring. Finally, the size classes covered by each life stage have been changed from the original models to reflect those size classes defined in an analysis of turtle excluder device effectiveness, where Epperly and Teas (1999) found that larger neritic immatures and adults were probably too large to fit through turtle excluder device openings.

The models are age classified, rather than stage classified, to allow for long time lags in population responses that are caused by delayed maturity and long stage lengths (Crowder et al. 1994). The annual survival rates for each model are based on Frazer (1986) and a model "fit" for oceanic immature annual survival to obtain a pre-1990 population growth rate of –5% per year (Crowder et al. 1994) (Table 16.3). The annual survival rates of each life stage had to be increased somewhat in Model 2 in order to obtain a "reasonable" oceanic survival rate, that is, < 95% per year. The original models by Crouse et al. (1987) and Crowder et al. (1994) used a primary sex ratio of 0.5. Foraging ground stud-
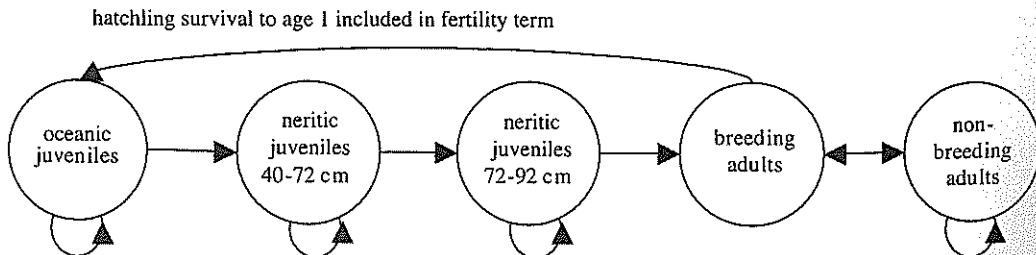

Figure 16.1. Life cycle graph of updated loggerhead matrix models.

Table 16.3.
Annual Survival Rates for Each Stage Used in Updated Loggerhead Matrix Models

	Oceanic Immature 5–45 cm	Small Neritic Immature 45–72 cm	Large Neritic Immature 72–92 cm	Nesting Females 92 cm	Nonnesting Females 92+
Model 1	0.745	0.6758	0.7425	0.8091	0.8091
Model 2	0.875	0.7	0.8	0.85	0.85

ies indicate there is a female bias along the Atlantic coast (Braun-McNeill et al. 2000a, 2000b; Wibbels et al. 1987), but because they are composed of multiple subpopulations, it is difficult to know the sex ratio of any individual population. It is likely that the proportion of females in the southern Florida subpopulation is higher than in the northern subpopulation and that the southern Florida subpopulation dominates the foraging ground studies. To be conservative in their model runs, the authors retained a primary sex ratio of 0.5, which probably more closely approximates the ratio of the northern subpopulation, although no data are available to confirm this.

The authors applied four different turtle excluder device (TED) effectiveness scenarios to the two models: (1) no TEDs (initial population growth = –5% per year), (2) TED-reduced mortality of small neritic immatures only, (3) TED-reduced mortality for small and large neritic immatures, and (4) TED-reduced mortality for neritic immatures and adults (both nesting and nonnesting). In previous models, it was assumed that all neritic turtles would have the same reduction in mortality due to turtle excluder devices (Crowder et al. 1994). According to an analysis of South Carolina strandings by Crowder et al. (1995), the number of dead turtles that stranded on beaches after turtle excluder devices were put in place was reduced by 30–40%. For this analysis, the authors used a mortality (= 1 minus annual survival) reduction of 30% for each affected stage.
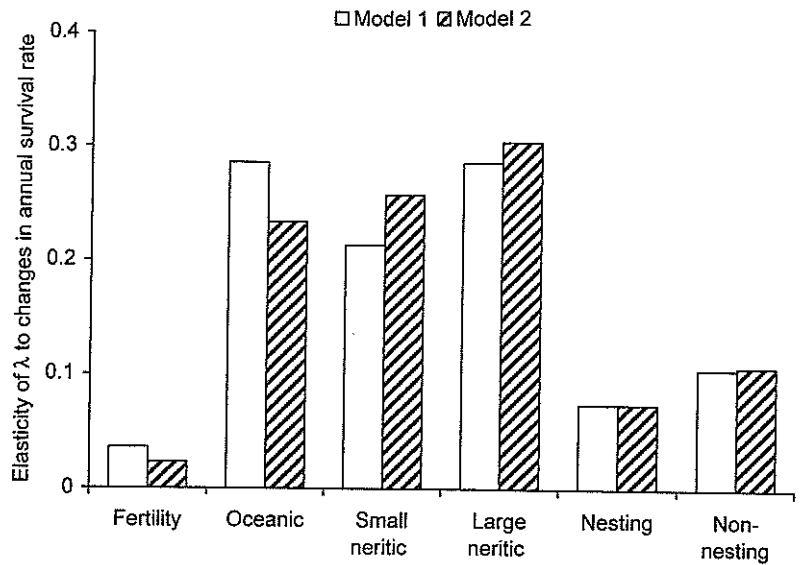
Results

Elasticity analysis is a method that compares the potential proportional change in population growth given a proportional change in each annual survival rate (de Kroon et al. 1986, 2000). Elasticities also reveal the proportional contribution of each matrix entry to the population growth rate. The elasticities in an age-based matrix can be added to get the total proportional contribution of survival for a given life stage (Figure 16.2). In age-structured models, the elasticity of λ to changes in immature stage survival is dependent on the number of age classes included in the stage (Caswell 2000; Heppell et al. 2000a). Thus, in Model 1, oceanic immatures and large neritic immatures have the same elasticity, which is higher than those of the other stages. In Model 2, small and large neritic immatures have longer stage lengths than the oceanic stage and, hence, higher elasticities. So stage length is an important factor when comparing the relative contributions of stage-specific survival rates.

Population growth rates, given in proportional change per year, were similar between the two models for each of the four turtle excluder device effectiveness scenarios (Figure 16.3), although greater population growth rates were predicted for Model 1. If turtle excluder devices only reduce the mortality of small neritic immature loggerheads, the population is not expected to increase over the long term. This is likely even if the mortality of small neritic immatures is reduced by a larger percentage, because mortality rates of large neritic immatures and adults would be too high to result in a population increase. Crowder et al. (1994) optimistically applied the same mortality reduction to all neritic stages, represented here by the fourth turtle excluder device effectiveness scenario. As with the original model, a 30% reduction in mortality of neritic immatures and adults

Figure 16.2. Elasticity analysis of two updated loggerhead matrix models, showing the relative proportional contribution of each survival rate to population growth. Stage lengths and survival rates for the two models are given in tables 16.2 and 16.3.


does result in a population increase for both Model 1 and Model 2, but the rate of increase is not large (1–2% per year). The later age at maturity and the longer generation time of Model 2 result in slower population growth.

Using the models given by the turtle excluder device effectiveness scenarios outlined above, the authors plotted the trajectories of nesting female population size through time to show the effects of time lags caused by long

stage lengths. All simulations started with a population of 2,000 nesters (1990 estimate; TEWG 1998) and the remaining population at a stable age distribution given by the baseline models (population growth = –5% per year). Because of uncertainties in population distribution and survival rates, these trajectories should be compared qualitatively and not used to predict actual population sizes through time. In both models, the change in nesters exhibits

Figure 16.3. Population growth rates with four turtle excluder device effectiveness scenarios. Turtle excluder devices reduce mortality by 30% for each stage affected: small neritic immature turtles; small and large neritic immatures; and small and large neritic immatures plus adults. None is no turtle excluder devices. Growth rate is expressed as proportional change per year $(\lambda - 1)$.
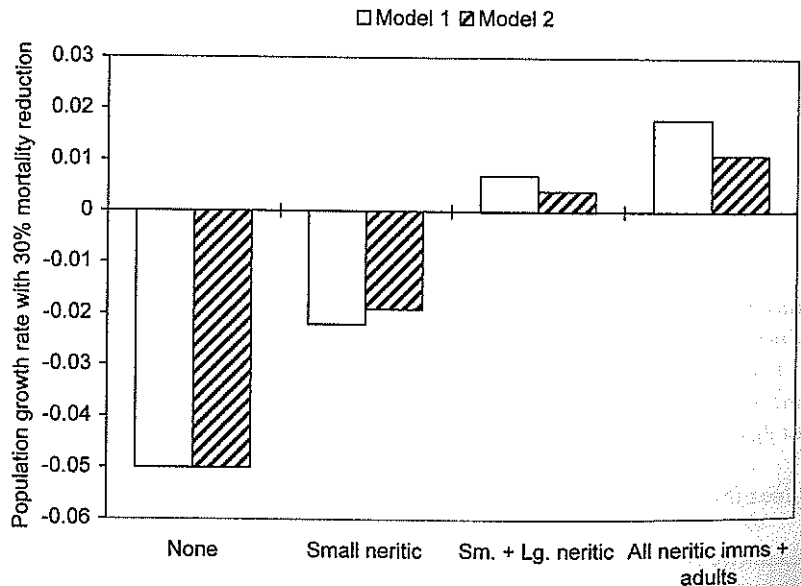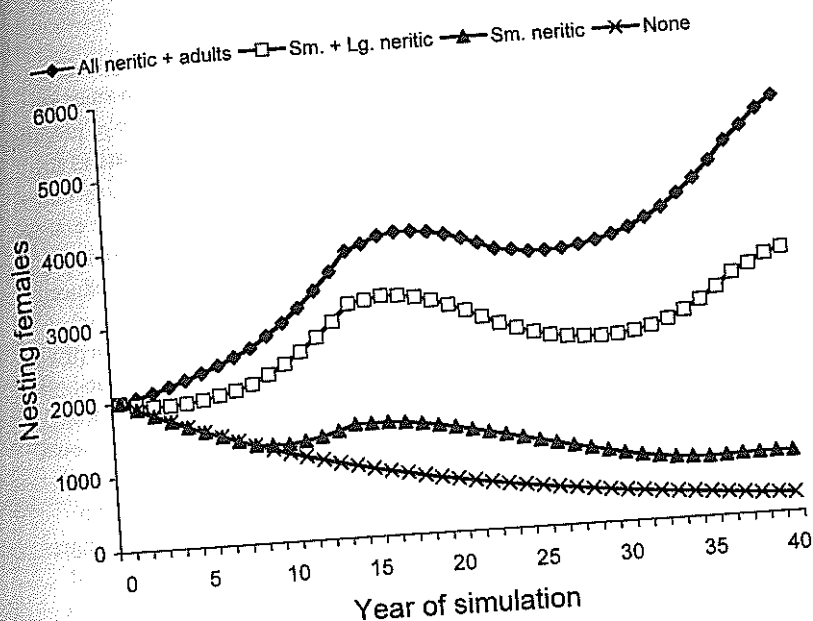
Figure 16.4. Population trajectory predicted by Model 1 with the four turtle excluder device effectiveness scenarios shown in Figure 16.3.

long amplitude "waves" in the population that are caused by shifts in the age distribution following perturbation (turtle excluder device implementation in year 0) (Figures 16.4 and 16.5). The longer time lag of Model 2 (25 years) delays the positive impact of decreased neritic stage mortality, but significant increases in nesting females are predicted after the 40-year simulation period if small and large neritic immatures

benefit from turtle excluder devices, or if all three stages benefit.

Conclusions from the Updated Models

The survival rates of the oceanic immature stage and neritic immature stages have a large impact on overall population growth in both of the updated models. Thus, small increases or decreases
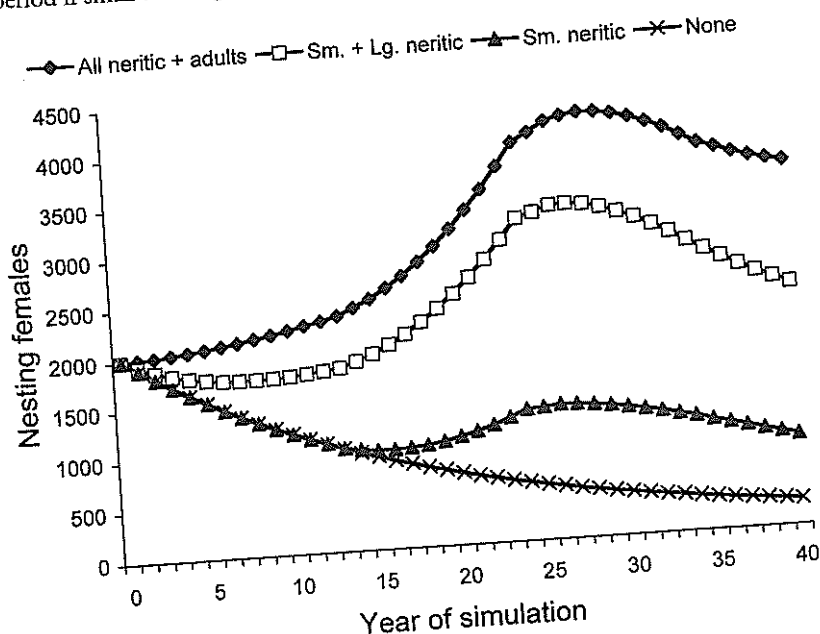

Figure 16.5. Population trajectory predicted by Model 2 with the four turtle excluder device effectiveness scenarios shown in Figure 16.3.

in the annual survival of either of these stages can have a dramatic effect on long-term population growth rates. The relative contribution to population growth of each immature stage depends on its stage length. Elasticity analysis should not be used to simply identify the "most sensitive" life stage, particularly if management policy is based purely on this result (Heppell et al. 2000c). The current estimate of an 8–10-year oceanic stage would make this the "most sensitive stage" in the original matrix models (as shown here in Model 1), but neritic immature growth rates also appear to be slower than previously estimated (Model 2). Until these uncertainties are further researched and a model that incorporates true growth rate variance can be constructed for U.S. loggerheads, updated models like these can only provide a rough comparative analysis of potential turtle excluder device effectiveness.

Time lags caused by late age at first reproduction and a long neritic immature stage will reduce the chances of observing an increase in nesting females for many years. Increases in recruitment to the neritic population are likely to be detected much sooner.

Discussion—Do We Need More Models and Why?

Conservation Concerns

Atlantic loggerheads continue to experience mortality due to human activities at all life stages. Because the loggerhead models have highlighted reductions in survival of both oceanic and neritic juveniles as serious management concerns, identification and reduction of mortality factors for these stages has taken on increased importance. These factors have recently been reviewed for loggerheads in U.S. Atlantic waters (NMFS 2001; TEWG 2000). All of the loggerhead modeling to date points to the oceanic juvenile stage as the first or second most sensitive to increases in mortality. Pelagic longlines, marine debris, and *Sargassum* harvesting are the major known threats. For neritic immature and adult turtles, shrimp, fish, and crab trawls; gill nets; pot lines; incidental hooking; takes by dredges and power plants; collisions with boats; and ingested debris are the

major known threats. While the loggerhead models suggest that population dynamics are most sensitive to increased mortality of juveniles and adults, populations cannot withstand sustained high losses of eggs and hatchlings either. It is unclear from the current models at exactly what point these losses become unsustainable, but by the time they are expressed as reduced adult nesting it may be too late to reverse 25–35 years of such impacts. Clearly the prudent alternative is to protect a significant amount of high quality nesting habitat now. The recovery plan for the U.S. nesting population of Atlantic loggerheads calls for 25% of coastal nesting habitat in public ownership (NMFS and USFWS 1991). While the loggerhead models and this discussion are focused primarily on North Atlantic loggerheads, the general principles and lessons learned should be applicable everywhere.

Incorporating Subpopulation Differences

The large contribution of the southern Florida subpopulation (10 times that of the northern subpopulation) is likely affecting sex ratios and the genetic distribution of loggerheads on foraging grounds. It is also possible that the southern Florida input is "masking" the lack of population recovery in the northern nesting populations. The authors speculated on the general structure of a population model that would take subpopulation differences into account (Figure 16.6). But parameterizing such a model to include this effect would require much more information about the relative proportions of different subpopulations that occur in different geographical areas.

Potential for More Instructive Models

With the rise of modern computers, the information contained in life tables allows the construction of mathematical models to examine the consequences to an imaginary population of altering its survival or fecundity schedules. One can employ a variety of methods from aggregated stage- or age-based models to individual-based and even spatially explicit models
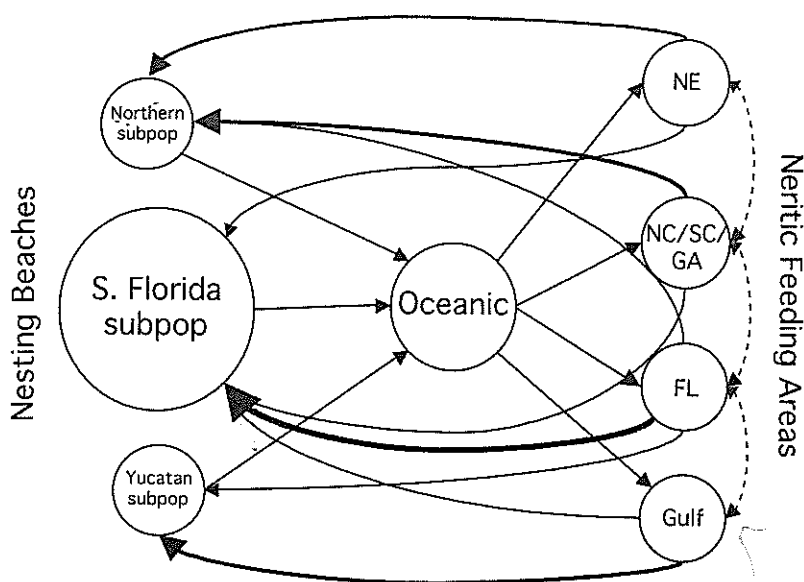
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Figure 16.6. Conceptual model for loggerheads that includes subpopulation differences. Arrows denote transitions between life stages and habitats (i.e., migration). Arrow widths denote relative contributions of different feeding areas to nesting populations, determined through genetic analysis. Additional arrows denoting adult migration to and from the nesting beaches are excluded for clarity. NE: northeast; NC: North Carolina; SC: South Carolina; GA: Georgia; FL: Florida; Gulf = Gulf of Mexico.

(DeAngelis and Gross 1992; Tuljapurkar and Caswell 1997). Even simple models have allowed researchers to ask questions about the relative importance of having precise and accurate information about the survival and fecundity of each life stage. That is, one can conduct sensitivity analyses and ask, "For which of the model inputs is it imperative to have more precise or more accurate information?" The models have also allowed researchers to examine the probable outcomes of various management scenarios. Unfortunately, the models will never be better than the information that is put into them. Until new information is gathered and synthesized on the demographic characteristics of loggerheads in the Western Atlantic, little progress will be made in developing more predictive models.

For example, most loggerhead biologists assume that loggerhead hatchlings from the western Atlantic beaches migrate to and inhabit eastern Atlantic areas as developmental habitat before returning to the western Atlantic at about half their adult size. Researchers already know from the work of Bjorndal et al. (2000) that growth rates of juvenile loggerheads in the eastern Atlantic are slower than predicted by the von Bertalanffy growth model. Thus, the age at maturity estimated by Frazer (1983a) and Frazer and Ehrhart (1985) for loggerheads might be much too low. This also calls into serious question the accuracy of the estimates of

juvenile survival rates that were based on using the von Bertalanffy equation to assign ages to juveniles in Frazer's (1983a, 1987) catch-curve analysis. Before further progress can be made with modeling Atlantic loggerhead populations, researchers need information on survival rates for juveniles at sea and new estimates of age at maturity and of adult survival since the initiation of turtle excluder devices.

There is little to be gained from constructing complex models if most of the parameters have no measured means or variances, and results obtained from such models can give a false sense of precision (Caughley 1994). Even heuristic models with a large number of unknowns may produce a myriad of results that are difficult to interpret. TEWG (2000) has made a number of research recommendations, many of which are aimed directly at resolving uncertain model parameters, including subpopulation differences, variable growth rates, and updated survival rate estimates. NMFS recognizes that new and better models can aid population recovery through improved management, but only if the models are based on sound empirical data.

Conclusions

Early sea turtle models by Frazer, Crouse, and Crowder provided important insights, but the

fact that research funding has not been available to improve these models is a cause for deep concern. The authors' minor efforts here to improve the existing models are merely adding bells and whistles. While some new data on growth and genetic composition of Atlantic loggerhead stocks have been collected, there have been no efforts to calculate new survival rates through mark-recapture studies. This is especially critical today, as turtle excluder devices are thought to have decreased mortality rates, but by an unknown proportion. As the Crouse et al. (1987) model clearly showed, model results can have a positive impact on policy and population recovery. Although the results from the early models are likely to be qualitatively robust, researchers should not be relying on heuristic analysis of possible population changes today based on survival rates calculated for a single subpopulation 30 years ago.

LITERATURE CITED

Aguilar, R., J. Mas, and X. Pastor. 1995. Impact of Spanish swordfish longline fisheries on the loggerhead sea turtle *Caretta caretta* populations in the western Mediterranean. NOAA Technical Memorandum NMFS-SEFSC-361:1–6.

Bass, A. L., S. P. Epperly, J. Braun, D. W. Owens, and R. M. Patterson. 1998. Natal origin and sex ratios of foraging sea turtles in the Pamlico-Albemarle Estuarine Complex. NOAA Technical Memorandum NMFS-SEFSC-415:137–138.

Bass, A. L., S.-M. Chow, and B. W. Bowen. 1999. Temporal variation in loggerhead strandings from Georgia. Final report to Georgia Department of Natural Resources. Gainesville: Department of Fisheries and Aquatic Sciences, University of Florida.

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821–841.

Bjorndal, K. A., and A. B. Bolten. 1988. Growth rates of juvenile loggerheads, *Caretta caretta*, in the southern Bahamas. Journal of Herpetology 22:480–481.

Bjorndal, K. A., A. B. Bolten, J. Gordon, and J. A. Camiñas. 1994. *Caretta caretta* (loggerhead) growth and pelagic movement. Herpetological Review 25:23–24.

Bjorndal, K. A., A. B. Bolten, and H. R. Martins. 2000. Somatic growth model of juvenile logger-

head sea turtles: Duration of the pelagic stage. Marine Ecology Progress Series 202:265–272.

Bolten, A. B., K. A. Bjorndal, and H. R. Martins. 1994. Life history model for the loggerhead sea turtle *(Caretta caretta)* populations in the Atlantic: Potential impacts of a longline fishery. NOAA Technical Memorandum NMFS-SWFC-201:48–55.

Bolten, A. B., K. A. Bjorndal, H. R. Martins, T. Dellinger, M. J. Biscoito, S. E. Encalada, and B. W. Bowen. 1998. Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. Ecological Applications 3:1–7.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology and Systematics 23:481–506.

Bowen, B. W. 1995. Tracking marine turtles with genetic markers. BioScience 45:528–534.

Bowen, B. W., J. C. Avise, J. I. Richardson, A. B. Meylan, D. Margaritoulis, and S. R. Hopkins-Murphy. 1993. Population structure of loggerhead turtles *(Caretta caretta)* in the northwestern Atlantic Ocean and Mediterranean Sea. Conservation Biology 7:834–844.

Braun-McNeill, J. B., S. P. Epperly, D. W. Owens, and R. M. Patterson. 2000a. Sex ratios of foraging sea turtles in the Pamlico-Albemarle Estuarine Complex, North Carolina, U.S.A. NOAA Technical Memorandum NMFS-SEFSC-436:121–122.

———. 2000b. Sex ratios of immature sea turtles: Does water temperature make a difference? NOAA Technical Memorandum NMFS-SEFSC-443:127–128.

Braun-McNeill, J., S. P. Epperly, L. Avens, and M. Snover. In review. A preliminary analysis of growth data of juvenile loggerhead *(Caretta caretta)* sea turtles from North Carolina, U.S.A.

Carr, A. 1986. Rips, FADS and little loggerheads. BioScience 36:92–100.

———. 1987. New perspectives on the pelagic stage of sea turtle development. Conservation Biology 1:103–121.

Caswell, H. 2000. Matrix population models, 2nd ed. Sunderland, Mass.: Sinauer Associates, Inc.

Caswell, H., and P. A. Werner. 1978. Transient behavior and life history analysis of teasel (*Dipsacus sylvestris* Huds.). Ecology 59:53–66.

Caswell, H., R. J. Naiman, and R. Morin. 1984. Evaluating the consequences of reproduction in complex salmonid life cycles. Aquaculture 43:123–134.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Crouse, D. T. 1999. The consequences of delayed maturity in a human-dominated world. American Fisheries Society Symposium 23:195–202.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423.

Crowder, L. 2000. Leatherback's survival will depend on an international effort. Nature 405:881.

Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4:437–445.

Crowder, L. B., S. R. Hopkins-Murphy, and A. Royle. 1995. Estimated effect of turtle excluder devices (TEDs) on loggerhead sea turtle strandings with implications for conservation. Copeia 1995:773–779.

DeAngelis, D. L., and L. J. Gross, editors. 1992. Individual-based models and approaches in ecology: Populations, communities and ecosystems. New York: Routledge, Chapman, and Hall.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: The relative contribution of demographic parameters to population growth rate. Ecology 67:1427–1431.

de Kroon, H., J. van Groenendael, and J. Ehrlen. 2000. Elasticities: A review of methods and model limitations. Ecology 81:607–618.

Eckert, S. A., D. T. Crouse, L. B. Crowder, M. Maceina, and A. Shah. 1994. Review of the Kemp's ridley sea turtle headstart experiment. Report to the National Marine Fisheries Service, based on a workshop at Galveston, Texas, 22–23 September 1992. NOAA Technical Memorandum NMFS-OPR-3.

Encalada, S. E., K. A. Bjorndal, A. B. Bolten, J. C. Zurita, B. Schroeder, E. Possardt, C. J. Sears, and B. W. Bowen. 1998. Population structure of loggerhead turtle (Caretta caretta) nesting colonies in the Atlantic and Mediterranean as inferred from mitochondrial DNA control region sequences. Marine Biology 130:567–575.

Epperly, S. P., and W. G. Teas. 1999. Evaluation of TED opening dimensions relative to size of turtles stranding in the Western North Atlantic. NOAA NMFS-SEFSC PRD-98/99-08.

Francisco, A. M., A. L. Bass, and B. W. Bowen. 1999. Genetic characterization of loggerhead turtles (Caretta caretta) nesting in Volusia County. Gainesville: Department of Fisheries and Aquatic Sciences, University of Florida.

Frazer, N. B. 1983a. Survivorship of adult female loggerhead sea turtles, Caretta caretta, nesting on Little Cumberland Island, Georgia, U.S.A. Herpetologica 39:436–447.

———. 1983b. Demography and life history evolution of the Atlantic loggerhead sea turtle, Caretta

caretta. Ph.D. Dissertation, University of Georgia, Athens.

———. 1986. Survival from egg to adulthood in a declining population of loggerhead turtles, Caretta caretta. Herpetologica 42:47–55.

———. 1987. Preliminary estimates of survivorship for loggerhead sea turtles (Caretta caretta). Journal of Herpetology 21:232–235.

Frazer, N. B., and L. M. Ehrhart. 1985. Preliminary growth models for green, Chelonia mydas, and loggerhead, Caretta caretta, turtles in the wild. Copeia 1985:73–79.

Frazer, N. B., and J. I. Richardson. 1985. Annual variation in clutch size and frequency for loggerhead turtles, Caretta caretta, nesting at Little Cumberland Island, Georgia, U.S.A. Herpetologica 41:246–251.

Groom, M. J., and M. A. Pascual. 1998. The analysis of population persistence: An outlook on the practice of viability analysis. In P. L. Fiedler and P. M. Kareiva (eds.). Conservation biology for the coming decade, 2nd ed., 4–27. New York: Chapman and Hall.

Heppell, S. S. 1997. On the importance of eggs. Marine Turtle Newsletter 76:6–8.

———. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998:367–375.

Heppell, S. S., C. J. Limpus, D. T. Crouse, N. B. Frazer, and L. B. Crowder. 1996a. Population model analysis for the loggerhead sea turtle, Caretta caretta, in Queensland. Wildlife Research (Australia) 23:143–159.

Heppell, S. S., D. T. Crouse, and L. B. Crowder. 1996b. A model evaluation of headstarting as a management tool for long-lived turtles. Ecological Applications 6:556–565.

Heppell, S. S., H. Caswell, and L. B. Crowder. 2000a. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. Ecology 81:654–665.

Heppell, S. S., D. T. Crouse, and L. B. Crowder. 2000b. Using matrix models to focus research and management efforts in conservation. In S. Ferson and M. Burgman (eds.). Quantitative Methods in Conservation Biology, 148–168. New York: Springer.

Heppell, S., C. Pfister, and H. de Kroon. 2000c. Elasticity analysis in population biology: Methods and applications. Ecology 81:605–606.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: Choice, dynamics and uncertainty. New York: Chapman and Hall.

Ito, R. Y., and W. A. Machado. 1999. Annual report of the Hawaii-based longline fishery for 1998.

NOAA/NMFS/SWFSC Administrative Report H-99-06.

Johnson, D. R., C. Yeung, and C. A. Brown. 1999. Estimates of marine mammal and marine turtle bycatch by the U.S. pelagic longline fleet in 1992–1997. NOAA Technical Memorandum NMFS-SEFSC-418.

Klinger, R. C., and J. A. Musick. 1995. Age and growth of loggerhead turtles (*Caretta caretta*) from Chesapeake Bay. Copeia 1995:205–209.

Laurent, L., J. Lescure, L. Excoffier, B. Bowen, M. Domingo, M. Hadjichristophorou, L. Kornaraki, and G. Trabuchet. 1993. Étude génétique des relations entre les populations méditerranéenne et atlantique d'une tortue marine (*Caretta caretta*) à l'aide d'un marqueur mitochondrial. Comptes Rendus de l'Academie des Sciences (Paris), Sciences de la Vie, Biologie et Pathologie Animale 316:1233–1239.

Laurent, L., P. Casale, M. N. Bradai, B. J. Godley, G. Gerosa, A. C. Broderick, W. Schroth, B. Schierwater, A. M. Levy, D. Freggii, E. M. Abd El-Mawla, D. A. Hadoud, H. E. Gomati, M. Domingo, M. Hadjichristophorou, L. Kornaraky, F. Demirayak, and Ch. Gautier. 1998. Molecular resolution of marine turtle stock composition in fishery bycatch: A case study in the Mediterranean. Molecular Ecology 7:1529–1542.

Maigret, J. 1983. Repartition des tortues de mer sur les cotes ouest Africaines. Bulletin of the Society for Herpetology 1983:22–34.

Márquez-M., R. 1990. FAO species catalogue. Vol. 11. Sea turtles of the world, an annotated and illustrated catalogue of sea turtle species known to date. FAO Fisheries Synopsis 125.

Mendonca, M. T. 1981. Comparative growth rates of wild immature *Chelonia mydas* and *Caretta caretta* in Florida. Journal of Herpetology 15:447–451.

NMFS and USFWS. 1991. Recovery plan for U.S. Atlantic populations of the loggerhead sea turtle (*Caretta caretta*). Silver Spring, Md.: National Marine Fisheries Service.

NMFS/SEFSC. 2001. Stock assessments of loggerhead and leatherback sea turtles and an assessment of the impact of the pelagic longline fishery on the loggerhead and leatherback sea turtles of the western North Atlantic. NOAA Technical Memorandum NMFS-SEFSC-455.

National Research Council. 1990. Decline of sea turtles: Causes and prevention. Washington, D.C.: National Academy Press.

Nishimura, W., and S. Nakahigashi. 1990. Incidental capture of sea turtles by Japanese research and training vessels: Results of a questionnaire. Marine Turtle Newsletter 51:1–4.

Norrgard, J. 1995. Determination of stock composition and natal origin of a juvenile loggerhead turtle population (*Caretta caretta*) in Chesapeake Bay using mitochondrial DNA analysis. M.A. Thesis, College of William and Mary, Williamsburg, Va.

Rankin-Baransky, K. C. 1997. Origin of loggerhead turtles in the western North Atlantic as determined by mtDNA analysis. M.S. Thesis, Drexel University, Philadelphia, Pa.

Richardson, T. H., J. I. Richardson, C. Ruckdeschel, and M. W. Dix. 1978. Remigration patterns of loggerhead sea turtles (*Caretta caretta*) nesting on Little Cumberland and Cumberland Island, Georgia. Florida Marine Research 33:39–44.

Sears, C. J. 1994. Preliminary genetic analysis of the population structure of Georgia loggerhead sea turtles. NOAA Technical Memorandum NMFS-SEFSC-351:135–139.

Sears, C. J., B. W. Bowen, R. W. Chapman, S. B. Galloway, S. R. Hopkins-Murphy, and C. M. Woodley. 1995. Demographic composition of the feeding population of juvenile loggerhead sea turtles (*Caretta caretta*) off Charleston, South Carolina: Evidence from mitochondrial DNA markers. Marine Biology 123:869–874.

Snover, M. L., A. A. Hohn, and S. A. Macko. 2000. Detecting the precise time at settlement from pelagic to benthic habitats in the loggerhead sea turtle, *Caretta caretta*. *In* H. J. Kalb and T. Wibbels (compilers). Proceedings of the 19th annual symposium on sea turtle biology and conservation, 174. NOAA Technical Memorandum NMFS-SEFSC-443.

Spotila, J. R., R. D. Reina, A. C. Steyermark, P. T. Plotkin, and F. R. Paladino. 2000. Pacific leatherback turtles face extinction. Nature 405:529–530.

TEWG. 1998. An assessment of the Kemp's ridley (*Lepidochelys kempii*) and loggerhead (*Caretta caretta*) sea turtle populations in the western North Atlantic. NOAA Technical Memorandum NMFS-SEFSC-409.

———. 2000. Assessment update for the Kemp's ridley and loggerhead sea turtle populations in the western North Atlantic. NOAA Technical Memorandum NMFS-SEFSC-444.

Tuljapurkar, S., and H. Caswell (eds.). 1997. Structured-population models in marine, terrestrial, and freshwater systems. New York: Chapman and Hall.

Weber, M., D. Crouse, R. Irvin, and S. Iudicello. 1995. Delay and denial: A political history of sea turtles and shrimp fishing. Washington, D.C.: Center for Marine Conservation.

Wibbels, T., D. W. Owens, Y. A. Morris, and M. S. Amoss. 1987. Sexing techniques and sex ratios for

immature loggerhead sea turtles captured along the Atlantic coast of the United States. NOAA Technical Report NMFS-53:65–73.

Wilbur, H. M. 1975. The evolutionary and mathematical demography of the turtle *Chrysemys picta.* Ecology 56:64–77.

Witzell, W. N. 1999. Distribution and relative abundance of sea turtles caught incidentally by the U.S. pelagic longline fleet in the western North Atlantic Ocean, 1992–95. Fisheries Bulletin 97:200–211.

Witzell, W. N., A. L. Bass, M. J. Bresette, D. A. Singewald, and J. C. Gorham. In preparation. Origin of immature loggerhead sea turtles *(Caretta caretta)* from Hutchinson Island, Florida: Evidence from mtDNA markers.